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Differential dispersal costs and sex-biased dispersal distance in a cooperatively breeding bird

Short title: Sex-biased dispersal in Seychelles warblers

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LAY SUMMARY

Why does the distance that animals disperse between their natal- and breeding territory usually differ between males and females? We show that in cooperatively breeding Seychelles warblers, males are reluctant to disperse and disperse less far than females. We suggest that this may be because for males, dispersal is more costly due to more aggression from other territorial males.

ABSTRACT

In most bird species, dispersal distance from the natal territory to a breeding territory is greater for females than for males. Two main hypotheses have been proposed to explain sex-biased dispersal: 1) it serves as an inbreeding-avoidance mechanism or 2) it is linked to a sex difference in resource-holding potential and territory establishment. Additionally, in species where individuals delay dispersal and become subordinates in a natal territory, differences in benefits of philopatry (e.g. territory inheritance, own reproduction) may also affect sex-biased dispersal. We show that in the group-living Seychelles warbler, *Acrocephalus sechellensis*, females disperse further to obtain a breeding position than do males. However, we found no evidence that female-biased dispersal distance can be explained by the above-mentioned hypotheses: further dispersal does not lead to less-related partners, both sexes defend and can inherit a territory, and subordinate females are more likely to obtain some reproduction than subordinate males. Instead, we provide evidence for a little-explored hypothesis based on sex differences in dispersal costs: namely that extra-territorial forays, pursued to search for limited vacancies, are more costly for males in terms of increased mortality, although the exact mechanism for this is unclear. In line with differential dispersal costs, males foray less far than females and often wait for local dispersal opportunities, ultimately resulting in a shorter average dispersal distance. Our results may help future studies in explaining sex-biased dispersal in social and perhaps also non-social species, and we suggest some mechanisms that may explain why sex-biased dispersal differs between species.

Key-words: cooperative breeding, delayed dispersal, habitat saturation, inbreeding, sex-biased dispersal

INTRODUCTION

In animals, the distance of dispersal from the natal territory or site to a place for independent breeding is often sex-biased (Greenwood 1980; Pusey 1987; Clarke, Sæther and Roskaft 1997). Sex-biased dispersal can have important implications for the dynamics and the genetic structure of populations (Aars and Ims 2000; Prugnolle and De Meeus 2002). Understanding its causes and consequences is therefore important to understanding how processes like kin cooperation and competition, resource defence and inbreeding avoidance can affect mating systems and population dynamics.

Two main non-exclusive hypotheses have been invoked to explain sex-biased dispersal (Greenwood 1980; Greenwood and Harvey 1982; Pusey 1987). First, the *inbreeding-avoidance* hypothesis predicts that the risk of mating with closely related individuals is reduced if dispersal distance is different between the sexes (Pusey and Wolf 1996; Perrin and Mazalov 2000; Perrin and Goudet 2001). This mechanism may especially be important in species with high levels of extra-pair mating, where females are predicted to disperse further to avoid running the risk of mating with their nearby extra-pair father. Males will not mate with their mother by dispersing short distances, as their mothers are always from within the natal territory. Second, the *resource-holding potential* hypothesis predicts that dispersal asymmetry between the sexes is a consequence of bias in the degree of advantage gained from familiarity with the area during intra-specific competition for resources towards the sex that defends those resources (Greenwood 1980; Pusey 1987), like is for example the case in territory establishment. Although both hypotheses have obtained some degree of support (Johnson and Gaines 1990; Bowler and Benton 2005; Lawson Handley and Perrin 2007), their respective importance remains unclear.

In species where opportunities for independent breeding are limited, such as family-living and cooperatively breeding species, subordinate individuals either have to wait in a home

territory for a breeding vacancy to arise nearby or to search for a vacancy in the population (Cockburn 1998). Waiting in a home territory may yield benefits to subordinate individuals (Stacey and Ligon 1991; Koenig & Dickinson 2004) and, if such 'benefits of philopatry' differ between males and females, this may lead to sex bias in motivation to search for an independent breeding vacancy, resulting in differences in the ultimate dispersal distance (Brown 1987; Cockburn 1998; Kingma et al. 2016a,b). As such, differences in the '*reproductive benefits of philopatry*' (i.e., the likelihood of obtaining a share in reproduction in the home territory, and/or inheriting the breeding position; e.g. Cockburn 1998; Kokko and Ekman 2002; Richardson et al. 2002) might explain sex-biased dispersal. Sex differences in the probability of territory inheritance may arise when the more competitive sex does not accept a related individual as a partner and could expel either an inheriting offspring or the remaining related breeder from the territory (e.g., Koenig and Stacey 1990; Nelson-Flower et al. 2012). Alternatively, or additionally, individuals who delay dispersal and remain in a home territory may gain '*energetic benefits of philopatry*', such as access to food. It is not immediately clear if and how such benefits differ between the sexes. However, the role that any such benefits play in explaining delayed dispersal would also depend on the costs of leaving, which may well be sex-specific (Perrin and Mazalov 2000; Gros et al. 2008).

In species both with and without delayed dispersal, searching for an independent breeding position involves extra-territorial forays through unfamiliar or unfavourable habitat (Reed et al. 1999). In a number of species it has been shown that such forays are associated with reductions in survival and body condition due to harassment by predators and conspecifics, and such costs have been invoked as explanation for delayed dispersal (e.g., Yaber and Rabenold 2002; Griesser et al. 2006; Ridley, Raihani & Nelson-Flower 2008; Ridley 2012; Kingma et al. 2016a). If such costs are different between both sexes, for example because of differences in conspicuousness to predators or because attacks by conspecifics may be more

100 frequently directed at the sex that threatens the reproduction of the resident individuals more,
101 they may well explain sex-biased dispersal distance. Whether this *dispersal-cost hypothesis* is
102 supported is unclear, however, partly because extra-territorial forays have received relatively
103 little empirical attention (Reed et al. 1999) and because studies of sex-biased dispersal
104 intrinsically focus on proximate and ultimate factors underlying dispersal, rather than the actual
105 movement *per se* (Lawson Handley and Perrin 2007). Together, these hypotheses, in addition
106 to the more conventional hypotheses of inbreeding avoidance and sex bias in resource-holding
107 potential, provide an interesting avenue to determine the importance of various social and
108 ecological factors for the evolution of sex-biased dispersal.

109 Here we tested all the above-mentioned hypotheses for female-biased dispersal distance
110 (see Table 1 and below) in the cooperatively breeding Seychelles warbler, *Acrocephalus*
111 *sechellensis*. This system is very suitable for testing these hypotheses for several reasons. First,
112 females on average disperse further from their natal territory than males (Eikenaar et al. 2008a).
113 Second, distinguishing dispersal from mortality is generally difficult (Koenig et al. 1996), but
114 since Seychelles warblers virtually never move between islands, individuals that have
115 disappeared from the study-population on Cousin Island almost certainly died (Komdeur et al.
116 2004). Third, in this long-term study population nearly all birds are individually marked and
117 followed throughout their life, so that their natal territory, dispersal behavior, relatedness to
118 other individuals, and dates of birth and death are known. Fourth, habitat saturation inhibits
119 independent breeding of subordinate individuals, but individuals can improve the likelihood of
120 obtaining an independent breeding position by extra-territorial forays to find a position
121 (Eikenaar et al. 2008a,b; Kingma et al. 2016a,b). Although such behaviors may be difficult to
122 assess in general (Reed et al. 1999), our detailed monitoring allows us to make inferences about
123 prospecting and floating. Fifth, many offspring are sired by males from outside the group
124 (~40%) who often live nearby (median distance = 2 territories; Richardson et al. 2002; Hadfield

et al. 2006), making the system suitable to test whether females disperse further than males to avoid incestuous matings with their extra-pair father.

We used a framework based on the above-mentioned hypotheses (see Table 1) to develop and test predictions of how different proximate and ultimate factors may explain female-biased dispersal distance in Seychelles warbler. Specifically, we assessed (1) whether dispersal over greater distance leads to the acquisition of a less-related partner, and whether this is especially the case for females who may mate with their extra-pair sire *(inbreeding-avoidance)*, (2) whether males and females differ in territory establishment (in terms of budding off part of the home territory) and defence (*resource-holding-potential*), (3) whether the probability of obtaining parentage as a subordinate and territory inheritance rates differ between male and female subordinates (*reproductive-benefits-of-philopatry*), and (4) whether the costs of finding an independent breeding territory differ between males and females in Seychelles warblers (*costly-dispersal*).

METHODS

Study system

We studied a population of ca. 320 individually colour-ringed Seychelles warblers on Cousin Island, Seychelles (29 ha; 04°20′S, 55°40′E) during the main breeding seasons (June-September) from 2003 until 2014. Each of the ca. 110 territories are occupied year-round by a dominant breeding pair, of which approximately half are accompanied by 1 to 4 independent subordinates. Dominant individuals rarely disperse and usually remain present in their territory until death (Hammers et al. 2015). Intruding conspecifics are physically attacked (Kingma *et al.* 2016a,b). Because of this, territory boundaries are easily determined based on border disputes between groups. Breeding vacancies are limited for both sexes because all suitable

habitat is occupied (Komdeur 1992) and Seychelles warblers are relatively long lived with mortality rates being similar for males and females (Brouwer et al. 2006); on average, the warblers live 5.5 years; Hammers et al. 2015). Individuals can improve their likelihood of finding a breeding vacancy by either temporarily (prospecting) or permanently (floating) leaving their territory to foray and search for vacancies across the island (Kingma *et al.* 2016b). Previous molecular analyses (Richardson et al. 2001, 2002, 2003, Hadfield et al 2006) revealed that ca. 40% of Seychelles warbler offspring are sired by breeder males from outside the territory, and while subordinate males rarely sire offspring, subordinate females often lay eggs in the nest of the breeding pair (Richardson et al. 2002); these findings have been confirmed across the more recent years spanning this study (Dugdale, Pant, Komdeur, Burke, Richardson, in prep).

In each season we performed regular censuses (at least weekly per territory) to identify for each individual the home territory (i.e., where birds were consistently observed foraging, performing reproductive tasks and/or involved in non-antagonistic interactions with other resident individuals) and breeding status (*dominant*: based on affiliative behavior between the pair members; *subordinate*: reproductively mature individuals but not involved in direct pair behaviors or initiation of breeding activities, or independent *juvenile*: 3-5 months old). Birds were captured using mist nets and each bird was given a unique combination of three colour rings and a numbered metal ring (if not already ringed). Body mass (± 0.1 g) and tarsus length (± 0.1 mm) were measured, and a small blood sample was taken to determine sex (following the protocol in Griffiths et al. 1998) and for genotyping (see below).

Inheritance, budding, dispersal, prospecting and floating

We determined whether each subordinate observed in a season was present by the beginning of the next season as a subordinate on the same territory, obtained a breeding position, or had

died. For individuals that obtained a breeding position, we determined whether this was achieved through inheritance of the natal territory, budding off part of it, or dispersal from that territory. We determined dispersal distance as the minimum number of territories that an individual had to cross between its natal territory and the territory where it obtained its breeding position (following Eikenaar et al. 2008b). A small number of individuals (n = 3 of 236 males and 5 of 240 females) settled as subordinates in a non-natal territory before obtaining a breeding position elsewhere, but we assess here the dispersal distance between the original natal territory and a breeding position only. The maximal possible distance that individuals could disperse over the island ranged from 9 to 16 territories (median = 12), and this did not differ between males (median: 12, n = 236) and females (median: 12, n = 240; generalized linear mixed model with maximum possible dispersal distance as a response variable, sex as an independent variable and 'natal-territory-identity' as a random variable: β = -0.004 ± 0.026, z = -0.15, P = 0.88).

Some individuals were observed or caught while prospecting (defined as individuals observed >2 territories away from their home territory and returned after prospecting to that territory) or floating (individuals only observed on non-resident territories multiple times throughout the season; see Kingma et al. 2016a,b for details). For each prospector we determined the maximum number of territories it was seen away from its home territory, similarly as for determining dispersal distance.

Statistical analyses

For the statistical analyses, models were fitted in R 3.2.0. (R development core-team, 2016) using the 'lme4' and 'lmerTest' packages (for linear mixed models and generalized linear mixed models; Bates et al. 2015; Kuznetsova et al. 2016), unless stated otherwise. Non-significant variables (P > 0.05) were sequentially excluded from the model, starting with the

least significant variable, until the model only contained significant variables. Values for non-significant variables were obtained by re-including them in turn in the final model to confirm that the order of exclusion did not change the results. Mean values and model estimates (β) are reported ± standard error (SE).

Sex-biased dispersal distance and prospecting behavior

We first confirmed findings from an earlier study (Eikenaar et al. 2008a), by testing whether dispersal distances between natal and subsequent breeding territory were different for males and females (n = 236 and 240, respectively) using a generalized linear mixed model with Poisson error, including 'natal-territory-identity' as random variable. Individuals who budded off part of their natal territory were classified as 'having dispersed one territory'.

We also tested whether the maximum distance that individuals prospected from the natal territory was different between males and females, using a generalized linear model with Poisson error.

Inbreeding avoidance

We tested whether dispersal distance and sex of the focal individual predicted the relatedness between that bird and its new partner (response variable) using a general linear mixed model with 'natal-territory-identity' as a random effect because in several cases multiple individuals from the same natal territory were included. We excluded seven pairs for which relatedness could not be determined due to an unsampled breeder. To test whether the effect of dispersal distance differed between males and females, we added the interaction between sex and distance. We excluded 41 individuals that inherited their natal territory from the analysis. Relatedness of dispersing individuals to their (first) dominant partner (R) was calculated using GenAlEx 6.5 (Peakall and Smouse 2012), using Queller and Goodnight (1989) estimation. We

225 determined relatedness between pair-members using 30 microsatellite markers, based on a
226 relatedness matrix including all possible dyadic combinations of all 544 birds in our study
227 (focal individuals and their partners, with the mean pairwise relatedness in the population being
228 equal to zero; see for details: Richardson et al. 2000, 2004; Spurgin et al. 2014; Bebbington et
229 al. 2016).

230 To assess whether females are likely to end up in an incestuous relationship with their
231 extra-group father if they only disperse to nearby territories, as predicted by Eikenaar et al.
232 (2008b), we used two approaches. First, we tested whether pair-relatedness was different
233 between females that obtained a partner after short-distance dispersal (1 or 2 territories from
234 their natal territory) and those that dispersed further, using a linear mixed model with 'natal-
235 territory-identity' as a random factor. Second, we tested whether pair-relatedness was different
236 between short-distance dispersing males and females using a similar model, predicting that if
237 females but not males could engage in an incestuous pair, short-distance dispersing females
238 would be more related to their partner than short-distance dispersing males. The distance of 1
239 or 2 territories for 'short-distance dispersal that may lead to incestuous mating' was chosen
240 because two territories is the median distance between an extra-group offspring's territory and
241 its sire (62% of extra-group fathers lived within two territories distance; Richardson et al.
242 2001). Note however, that the results are similar if this distance would be chosen differently,
243 because females who dispersed further did not pair with less related males (see Fig. 1b).

244

245 *Resource-holding potential*

246 To assess whether males and females differ in resource-holding potential, we used three
247 approaches (Table 1). First, subordinates Seychelles warblers may bud-off part of their territory
248 in which they are subordinate, in order to then attract a partner and breed independently. We
249 assessed whether sex predicted whether a subordinate obtained a territory by budding (using a

generalized linear mixed models with binomial error). Second, we analysed two probable determinants of sex differences in resource-holding potential: we assessed whether breeding males were larger and/or heavier than breeding females. We compared tarsus length (averaged if an individual was measured more than once) of males and females using a t-test. Subsequently, using all catches of each individual, we tested in a linear mixed model whether body mass (as response variable) was different between the sexes and added 'individual-identity', year and 'resident-territory-identity' as random factors and time [morning (6:34-10:00), midday (10:00-14:00), afternoon (14:00-19:10)] of capture as an independent variable to account for temporal and spatial variation in body mass. Third, using 121 opportunistically observed antagonistic interactions (observed during weekly censuses in each territory) between (identified) resident individuals and intruders, we determined whether male residents were more likely to be involved in antagonistic interactions than female residents using a binomial test.

Reproductive benefits of philopatry (parentage acquisition and territory inheritance)

Previously, it was shown that parentage success was substantially higher for female than male subordinates (Richardson et al. 2002), so that we can exclude this factor as an explanation for female-biased dispersal.

To assess whether the chances of territory inheritance are different for males and females, we used a number of approaches. First, for 96 territory vacancies where a subordinate was resident in a natal territory at the time a vacancy arose, we tested directly whether inheritance occurred more for female vacancies than for male vacancies using a χ^2-test. Second, we used a generalized linear mixed model to test whether individuals were more related to the opposite-sex breeder (response variable) if they inherited than if obtained a breeding position in another territory (i.e. through budding or dispersal), and tested whether this effect was

different between the sexes (included as independent variables and their interaction), including 'natal-territory-identity' of the focal individual as a random effect, since multiple individuals from the same territory were included. We excluded seven pairs for which relatedness could not be determined due to an unsampled breeder. Third, if males can expel a female but not vice versa, males should be more likely than females to inherit the territory with a related opposite-sex breeder. This is because males may expel their mother or sister, but females not their father or brother. Therefore, we tested whether the likelihood that subordinates filled a vacancy in their home territory (response variable) was dependent on the interaction between the sex of the subordinate and whether the opposite-sex breeder was related or not (first-order relative; based on social pedigree data). We removed one individual for which it was unknown whether the remaining breeder was related and 18 cases where more than one same-sex subordinate was present, as the presence of a same-sex subordinate reduces the chance that an individual would inherit the territory which would make it difficult to determine whether they did not inherit because they were related or because there was another subordinate present. Fourth, to determine whether the probability of staying as breeder after inheriting a position with a related partner was different between sexes, we determined whether females in incestuous pairs were more likely to divorce and leave than males.

Costly dispersal

In order to make inferences about sex-biased costs of dispersal, we tested whether male and female prospectors / floaters differed in the probability that before the next breeding season they (1) died (Fisher exact test) and (2) obtained a breeding position (χ^2 test; including individuals who died). As individuals only prospect or float before they are two years of age (see Kingma et al. 2016b), we restricted the analyses to birds younger than two years. In each season we determined whether individuals prospected or floated (see Kingma et al. 2016b for

details), and each individual was included in only one season, as only one female was observed prospecting for two years in a row (for which only the first season was included).

On occasion, foraying birds were caught opportunistically together with resident territory owners while they were involved in intraspecific chases (Kingma et al. 2016a). Therefore, to make inferences about whether foraying males were more often attacked by territory owners than foraying females, we tested whether foraying (prospecting and floating combined) males were more often caught with resident territory owners than foraying female (using all catches). We fitted a GLMM with 'bird-identity' as a random factor to account for multiple inclusions of individuals, whether or not an individual was caught with a resident individual as a response variable, and whether individuals prospected or floated, and sex (and their interaction), as independent variables.

Ethical note

All protocols conformed to legal requirements for use of animals in research and were approved by Seychelles Department of Environment and Seychelles Bureau of Standards (permit: A0157).

RESULTS

Routes to breeding

Most individuals obtained a breeding position by dispersing from their natal territory to a neighboring territory ('shifting') or further (Table 2). A small number of individuals inherited their natal territory (8.6%) or budded off part of it (2.5%).

Sex-biased dispersal distance and prospecting behavior

To test for sex bias in dispersal distance and prospecting behavior we compared these two measures between males and females. Females dispersed further from their natal territory than males (Fig. 1a). Females (median = 5 territories distance; range = 3-12) were also observed prospecting further than males (median = 3; range = 3-6; β = 0.460 ± 0.156, z = 2.95, P = 0.003). We have shown elsewhere that females prospect more often than males (annually 19% of 175 females and 9% of 162 males; Kingma et al. 2016b).

Inbreeding avoidance

Inbreeding avoidance is generally hypothesized to underlie sex-biased dispersal distance. However, dispersal distance (excluding inheriting individuals) did not affect the relatedness of the resulting breeding pair and this was similar for male and female dispersers (Table 3a; Fig. 1b).

If females disperse further to avoid the risk of mating incestuously with an extra-group father (ca. 40% of offspring are sired by nearby extra-group males in Seychelles warblers; Richardson et al. 2001), then we would expect to find that short-distance dispersal by females would be more likely to result in incestuous pairs. However, short-distance dispersing females were not more related to their new partner (R = 0.021 ± 0.032, n = 57) than further-dispersing females (R = 0.008 ± 0.018, n = 156, Table 3c) or short-distance dispersing males (R = 0.032 ± 0.017, n = 142; Table 3d).

Resource-holding potential

Although males tended to be more likely to bud off part of their natal territory than females (3.8 vs 1.3% of individuals; Table 2), this effect was not significant (β = 1.142 ± 0.673, t = 1.70, P = 0.09), and budding was rare overall (overall only 2.5% of individuals obtained a breeding position this way).

Tarsus length and body mass were used as measures of competitive ability and resource-holding potential. On average, males (25.9 ± 0.04 mm, n = 309) had a 6.3% longer tarsus length than females (24.4 ± 0.03 mm, n = 274; t = -29.96, $P < 0.001$). Similarly, males (mean mass = 16.5 ± 0.03 g, n = 784 catches) were on average 9.6% heavier than females (15.0 ± 0.04 g; n = 576; β = -1.425 ± 0.060, t = -23.95, $P < 0.001$; correcting for time of capture (relative to morning): midday: β = 0.053 ± 0.056, t = 0.948, P = 0.34, afternoon: β = 0.255 ± 0.055, t = 4.65, $P < 0.001$).

Despite the asymmetry in size, however, both sexes were equally represented in agonistic interactions with intruders (62 of 121 attacks (51%) were performed by females and 59 (49%) by males; binomial exact test: P = 0.86). This included attacks by 19 subordinates (10 females, 9 males), but excluding these did not change the result (P = 0.92).

Reproductive benefits of philopatry (parentage acquisition and territory inheritance)

If the reproductive benefits of philopatry (parentage acquisition and territory inheritance) are different between the sexes, then this might lead to sex-biased dispersal distance because the philopatric sex may only disperse if a nearby vacancy arises, whereas the dispersing sex might actively search for a vacancy throughout the population. As we could exclude differential parentage acquisition by subordinates as a mechanism based on previous research (female subordinates are more likely to reproduce than male subordinates; Richardson et al. 2002), we tested subsequently whether females were more likely to inherit the territory than males. This was, however, not the case. First, the chances of territory inheritance are equal for males and females: overall, 41 of the 476 breeding vacancies (8.6%) were filled by inheritance (Fig. 1a; Table 2), and if the respective-sex subordinate was present, then inheritance was equally likely for female (24 of 56 cases; 42.9%) and male vacancies (17 of 40 cases, 42.5%; $\chi^2_1 < 0.01$, P = 0.97). Second, since most subordinates are retained offspring, individuals were much more

related to their partner if they had inherited a breeding position in their home territory (R = 0.222 ± 0.039, n = 41) compared to individuals who dispersed to a breeding position (R = 0.020 ± 0.010, n = 428). However, this effect was not different between males and females (Table 3b, Fig. 1b). Third, the likelihood of filling a vacancy in the resident territory tended to be higher when subordinates were unrelated to the opposite-sex breeder (10/20, 50.0%) than when the remaining breeder was a first-order relative (18/57, 31.6%; β = -0.773 ± 0.530) but this effect was not significant (t = -1.46, P = 0.15), and did not depend on the sex of the subordinate (interaction: β = 1.749 ± 1.163, z = 1.50, P = 0.13). Breeding males were equally likely to accept a first-order relative as a partner (in 9/32 cases; 28.1%) as breeding females (in 9/25 cases; 36.0%; χ^2_1 = 0.321, P = 0.57). Fourth, although the small sample of divorcing incestuous pairs did not permit adequate statistical testing, only 1/8 father–daughter pairings, 3/8 mother–son pairings and 0/2 sibling pairings ended in divorce, where in two cases the female left (daughter and mother) and in two cases the son left.

Costly dispersal

By assessing sex differences in mortality and intraspecific interactions of floaters and prospectors, we studied the potential sex-biased costs of dispersal. Male floaters were significantly more likely to die than female floaters before the beginning of the next season (Fig. 2), and male floaters tended to be less likely to obtain a breeding position before the beginning of the next season (47% of 15 individuals) than female floaters (79% of 19) (although this result was not significant; χ^2_1 = 2.51, P = 0.11). Mortality rates were similar for both males and females that engaged in temporary prospecting trips (before returning to their home territory; Fig. 2), and the chance to obtain a breeding position before the beginning of the next season was not different between male (62% of 13) and female (54% of 39) prospectors (χ^2_1 = 0.01, P = 0.94). Male forayers (prospectors and floaters combined) were nearly twice as

often caught with a resident individual (29% of 24 catches) than female forayers (15% of 39 catches) but this effect was not statistically significant, either when including only 'sex' as explanatory variable (β = 0.804 ± 0.658, z = 1.22, P = 0.22) or sex as an interaction with whether individuals prospected or floated (β = -2.465 ± 1.665, z = -1.48, P = 0.14). The likelihood of being caught with a resident individual, did not differ between prospectors (20% of 35 individuals) and floaters (21% of 28; β = 0.206 ± 0.744, z = -0.28, P = 0.78).

DISCUSSION

Sex-biased dispersal distance in Seychelles warblers

In line with many studies (see Greenwood 1980) and with previous work on Seychelles warblers (Eikenaar et al. 2008a), we show that female subordinate Seychelles warblers disperse further from their natal territory to obtain a breeding position than males. This effect was not the result of females floating more often (i.e. permanently leaving a natal territory to search for a vacancy, likely occurring because of eviction by breeders; Eikenaar et al. 2007, Kingma et al. 2016b). However, female Seychelles warblers engage in temporary prospecting trips more often than males (19% vs 9%; Kingma et al. 2016b) and they prospect over larger distances than males (this study; see also Eikenaar et al. 2008a). This suggests that males generally remain as subordinates within a territory and explains why males often shift to a nearby vacancy when the opportunity arises (Fig. 1a; Table 2), whereas females more often actively search for such vacancies, resulting in a breeding position further afield. There are several potential explanations for sex-biased dispersal (Table 1), and below we discuss whether these can explain sex-biased dispersal distance in Seychelles warblers.

Benefits of philopatry, incest and inbreeding avoidance, and resource-holding potential

424 We tested the predictions of several hypotheses for sex-biased dispersal (Table 1), but the
425 results suggest that most of these hypotheses can be discounted in Seychelles warblers.

426 Sex-biased dispersal in species where subordinate individuals delay dispersal is
427 hypothesized to be based on differences in reproductive benefits-of-philopatry (i.e., in
428 reproduction as subordinate, territory inheritance or differences in competitive ability and
429 resource holding potential; Greenwood 1980; Zack and Rabenold 1989; Richardson et al.
430 2002). Our results suggest that we can rule out sex differences in reproductive benefits gained
431 by subordinates as an explanation for female-biased dispersal distance in Seychelles warblers:
432 subordinate females are more likely to gain parentage than subordinate males (Richardson et
433 al. 2001; Richardson et al. 2002), and territory inheritance is rare (8.6% of positions) and
434 achieved equally by males and females (Table 2). Furthermore, although incest avoidance
435 inhibits territory inheritance to some extent (whether or not the opposite-sex breeder was a
436 social parent tended to predict ($P = 0.06$) whether subordinates inherited), incestuous pairs are
437 formed in ca. 30% of the cases and this was not more likely for female subordinates than for
438 males. Moreover, although the sample size was small, incestuous pairings did not always end
439 in divorce (only in 4 of 18 cases) and, importantly, were not more likely to end in a female
440 leaving than a male. This suggests that males are not necessarily dominant over females and
441 that this cannot explain female-biased dispersal distance in this species. Similarly, although
442 males are larger and heavier, males did not appear to be more engaged in territory defence than
443 females (as is, for example, the case in some migratory species where males arrive earlier at
444 the breeding ground to establish territories; Arlt and Pärt 2008), leaving the 'resource-holding
445 potential hypothesis' unlikely as a direct explanation for our results. The latter is also confirmed
446 by observations that, after the disappearance of a breeding male, females are capable of holding
447 the territory until she pairs with a new male (median duration until the male vacancy was filled
448 in an experimental removal of breeding males was 2 days; Eikenaar et al. 2009). Perhaps the

449 relatively limited importance of resource-holding potential in Seychelles warblers is not
450 surprising since the habitat is saturated, territories are stable year round and very few new
451 territories are ever established (of the 476 cases where a subordinate became breeder, only 44
452 (9.2%) were obtained by establishing a new territory, of which 12 (2.5%) were budders). These
453 results indicate that territory establishment is difficult for individuals in the Seychelles warbler
454 system, especially compared to many other seasonally-breeding species which establish a new
455 territory every year, and where sex-biased dispersal may therefore be more likely explained by
456 differences in competitive ability (see Arlt & Pärt 2008 for an example). Thus, overall, these
457 results suggest that differences in reproductive benefits for philopatric individuals and
458 resource-holding potential cannot explain sex-biased dispersal distance in Seychelles warblers.
459 A previous study suggested that inbreeding avoidance may underlie sex-biased natal
460 dispersal in Seychelles warblers (Eikenaar et al. 2008a). Based on considerable levels of extra-
461 pair paternity in this species (~40% of offspring; Richardson et al. 2001), Eikenaar et al.
462 (2008a) hypothesized that females might generally disperse further than males because females
463 who pair with local individuals risk pairing incestuously with their extra-pair father. Although
464 females are indeed less likely to disperse to territories in the close vicinity (Fig. 1a), our
465 investigation of relatedness of breeding pairs in relation to dispersal distance does not support
466 this hypothesis. First, females pairing with a male within one or two territories of their natal
467 territory were not more related to that partner than either subordinate males pairing with a
468 female within a similar distance or females dispersing over a larger distances (Fig. 1b), as
469 would be expected if females had a high likelihood of pairing with an extra-pair father.
470 Although this finding could be explained by short-distance dispersing individuals avoiding
471 related individuals as partners, the evidence indicates that Seychelles warblers do not avoid
472 inbreeding (ca. 5% of offspring are a result of incestuous pairing; Richardson et al. 2004) and
473 Eikenaar et al. (2008b) show that subordinate Seychelles warbler females are generally not

more related to neighboring males than male subordinates to neighboring females. Combined, this suggests that the risk to engage in an incestuous pair for females dispersing over a short distance is actually negligible. Second, although territory inheritance did frequently result in incestuous pairs (see above), the distance that females and males dispersed did not predict the relatedness of the resulting breeding pair, suggesting that inbreeding-avoidance does not underlie sex-biased dispersal distance in this species.

Our finding that sex-biased dispersal is unlikely to function as an inbreeding avoiding mechanism is in line with the fact that inbreeding does not appear to be avoided in Seychelles warblers in general (Eikenaar et al. 2008b). Perhaps one explanation for this is that the importance of obtaining a breeding position outweighs the costs of inbreeding (which in Seychelles warblers can be observed in faster telomere shortening; Bebbington et al. 2016). Likewise, individuals engage in incestuous pairs in many other cooperatively breeding animals when faced with habitat saturation (e.g. Nielsen et al. 2012; Kingma et al. 2013; Nichols et al. 2014; but see e.g. Koenig et al. 1998). It would be interesting, for example by using meta-analyses, to determine whether the variation in the relative importance of sex-biased dispersal as inbreeding avoidance mechanism is at least partially determined by the degree of habitat saturation.

Costly dispersal

Mortality rates are not different between breeder male and female Seychelles warblers (Brouwer et al. 2006) and finding a vacancy is therefore equally difficult for males and female floaters (Kingma et al. 2016b). Given this, our finding of lower mortality of female compared to male floaters suggests that females may be more tolerated than males outside their home territory. These differences in the costs of searching for an independent breeding territory may underlie the lower rate of prospecting by male subordinate Seychelles warblers than females,

resulting in a shorter ultimate dispersal distance. The survival costs of prospecting did not differ between the sexes, but this may well be explained by prospecting individuals being able to return to their home territory after an unsuccessful prospecting trip, thereby obtaining the benefits of philopatry like nepotistic benefits facilitating access to food (Kingma et al. 2016b). Nonetheless, several findings suggest that extra-territorial movement is more costly for male than for female Seychelles warbles. First, males experienced a higher mortality cost of floating than females (Fig. 2). Differential costs of floating are generally difficult to tease apart from variation in quality of individuals that leave (i.e. floaters may have been of poorer quality). However, that subordinate male Seychelles warblers (1) search for vacancies (by means of prospecting) less often than females (Kingma et al. 2016), (2) disperse less far in densely-populated areas with more competitors (but females do not) (Eikenaar et al. (2008a), and (3) obtain a breeding position at an older age than females (Eikenaar et al. 2009), support the prediction that males are reluctant to leave voluntarily because of relatively high costs. While we can rule out predation (predation of adults is absent in this system), the exact mechanism causing higher costs of dispersal for males remains, as yet, unresolved. Although statistically not significant (with a small sample size), our observation that foraying male subordinates were nearly twice as likely to be caught with an individual resident in the intruded territory may indicate that males are attacked more often than females. Males may pose a greater threat to parentage of territory owners (e.g. due to extra-pair mating), but females are equally involved in territory defence and such sex-biased costs would only manifest during a brief 'fertile' period when individuals initiate breeding. Nonetheless, in the Seychelles warbler female subordinates often breed with the dominant pair (Richardson et al. 2003), so additional subordinate females appear to be less threatening to the dominant pair than an additional male subordinate, who may gain reproductive success at the breeding male's cost. The underlying mechanism generating the sex–biased dispersal costs, and to what extent these costs apply in other species

where the habitat is not saturated and where subordinate individuals cannot reproduce, is an interesting topic for further investigation. Ultimately, however, our results suggest that the fact that males often disperse only one or two territories can be explained by the relatively high costs of extra-territorial movement driving males to wait for local opportunities to disperse. Thus, asymmetry in costs of dispersal may explain sex-biased dispersal distance in this, and possibly other species (see also Perrin and Mazalov 2000; Gros et al. 2008; Pakanen et al. 2016 As these costs can be predicted to be especially high in species with habitat saturation, it would be worthwhile to compare the sex-specific costs of dispersal in other species, with and without habitat saturation, and how this relates to sex-biased dispersal. Perhaps such analyses, as discussed above for inbreeding avoidance, will help us understand why the mechanisms of sex-biased dispersal differ between different species.

Conclusions

We conclude that sex-biased dispersal distance in Seychelles warblers is unlikely to support the currently often invoked hypotheses (see Table 1). Female-biased dispersal distance does not seem to be explained by inbreeding-avoidance and differences in reproductive benefits of philopatry and resource-holding potential. Instead, our data suggest that dispersal attempts are more costly for males than for females. This may explain why selection favours reduced male subordinate extra-territorial movement required to find a breeding vacancy, which in turn likely leads to reduced dispersal distances and later acquisition of a breeding position (Eikenaar et al. 2009). This additional mechanistic explanation may not only shed light on sex-biased dispersal in family-living and cooperatively breeding species, but costs associated with searching for an independent breeding position may potentially also play a role in dispersal strategies in non-social species.

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DATA ACCESSIBILITY

Analyses reported in this article can be reproduced using the data provided by Kingma et al. (2017)

REFERENCES

Aars J, Ims RA. 2000. Population dynamics and genetic consequences of spatial density-dependent dispersal in patchy populations. Am Nat. 155:252–265.

573 Arlt D, Pärt T. 2008. Sex-biased dispersal: a result of a sex difference in breeding site
574 availability. Am Nat. 171:844-850.
575 Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using
576 lme4. J Stat Softw. 67:1-48.
577 Bebbington K, Spurgin LG, Fairfield EA, Dugdale HL, Komdeur J, Burke T, Richardson DS.
578 2016. Telomere length reveals cumulative individual and transgenerational inbreeding
579 effects in a passerine bird. Mol Ecol. 25:2949-2960.
580 Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating
581 individual behaviour to spatial dynamics. Biol Rev. 80:205-225.
582 Brown JL. 1987. Helping and communal breeding in birds. Princeton: Princeton University
583 Press.
584 Clarke AL, Sæther B-E, Roskaft E. 1997. Sex biases in avian dispersal: a reappraisal. Oikos.
585 79:429–438.
586 Cockburn A. 1998. Evolution of helping behaviour in cooperatively breeding birds. Ann Rev
587 Ecol Syst. 29:141–177.
588 Eikenaar C, Richardson DS, Brouwer L, Komdeur J. 2008a. Sex biased natal dispersal in a
589 closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*. J Avian
590 Biol. 39:73-80.
591 Eikenaar C, Komdeur J, Richardson DS. 2008b. Natal dispersal patterns are not associated with
592 inbreeding avoidance in the Seychelles Warbler. J Evol Biol. 21:1106-1116.
593 Eikenaar C, Richardson DS, Brouwer L, Bristol R, Komdeur J. 2009. Experimental evaluation
594 of sex differences in territory acquisition in a cooperatively breeding bird. Behav Ecol.
595 20:207-214.
596 Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. Ann Rev Ecol
597 Syst. 13:1-21.

598 Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim
599 Behav. 28:1140-1162.
600 Griesser M, Nystrand M, Ekman J. 2006. Reduced mortality selects for family cohesion in a
601 social species. Proc R Soc Lond B 273:1881–1886.
602 Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. Mol Ecol.
603 7:1071–1075.
604 Gros A, Hovestadt T, Poethke HJ. 2008. Evolution of sex-biased dispersal: The role of sex-
605 specific dispersal costs, demographic stochasticity, and inbreeding. Ecol Model.
606 219:226-233.
607 Hadfield JD, Richardson DS, Burke T. 2006. Towards unbiased parentage assignment:
608 combining genetic, behavioural and spatial data in a Bayesian framework. Mol Ecol.
609 15:3715-3730.
610 Hammers M, Kingma SA, Bebbington K, Van de Crommenacker J, Spurgin L, Richardson DS,
611 Komdeur J. 2015. Senescence in the wild: insights from a long-term study on Seychelles
612 warblers. Exp Geront. 71:69-79.
613 Johnson ML, Gaines MS. 1990. Evolution of dispersal: theoretical models and empirical tests
614 using birds and mammals. Ann Rev Ecol Syst. 21:449–480.
615 Kingma SA, Hall ML, Peters A. 2013. Breeding synchronization facilitates extrapair mating
616 for inbreeding avoidance. Behav Ecol. 24:1390-1397.
617 Kingma SA, Komdeur J, Hammers M, Richardson DS. 2016a. The cost of prospecting for
618 dispersal opportunities in a social bird. Biol Lett. 10.1098/rsbl.2016.0316.
619 Kingma SA, Bebbington K, Hammers M, Richardson DS, Komdeur J. 2016b. Delayed
620 dispersal and the costs and benefits of different routes to independent breeding in a
621 cooperatively breeding bird. Evolution. DOI: 10.1111/evo.13071.

622 Kingma SA, Komdeur J, Burke T, Richardson DS. 2017. Data from: Differential dispersal costs
623 and sex-biased dispersal distance in a cooperatively breeding bird. Dryad Digital
624 Repository. http://dx.doi.org/10.5061/dryad.sv069.
625 Kuznetsova A, Brockhoff PB, Christensen RHB. 2016. lmerTest: Tests in linear mixed effects
626 models. R package version 2.0-30. https://CRAN.R-project.org/package=lmerTest
627 Koenig WD, Dickinson J. 2004. Ecology and evolution of cooperative breeding birds.
628 Cambridge: Cambridge University Press.
629 Koenig WD, Van Vuren D, Hooge PN. 1996. Detectability, philopatry, and the distribution of
630 dispersal distances in vertebrates. Trends Ecol Evol. 11:514-517.
631 Koenig WD, Stacey PB. 1990. Acorn woodpeckers: group-living and food storage under
632 contrasting ecological conditions. In: Stacey PB, Koenig WD, editors. Cooperative
633 breeding in birds: long-term studies of ecology and behaviour. Cambridge: Cambridge
634 University Press. p. 413-453.
635 Koenig WD, Haydock J, Stanback MT. 1998. Reproductive roles in the cooperatively breeding
636 acorn woodpecker: incest avoidance versus reproductive competition. Am Nat. 151:243–
637 255.
638 Kokko H, Ekman J. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe
639 havens, and ecological constraints. Am Nat. 160:468-484.
640 Komdeur J. 1992. Importance of habitat saturation and territory quality for the evolution of
641 cooperative breeding in the Seychelles warbler. Nature. 358:493–495.
642 Komdeur J, Piersma T, Kraaijeveld K, Kraaijeveld-Smit F, Richardson DS. 2004. Why
643 Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there?
644 Ibis. 146:298-302.
645 Lawson Handley LJ, Perrin N. 2007. Advances in our understanding of mammalian sex-biased
646 dispersal. Mol Ecol. 16:1559-1578.

647 Nelson-Flower MJ, Hockey PAR, O'Ryan C, Ridley AR. 2012. Inbreeding avoidance
648 mechanisms: dispersal dynamics in cooperatively breeding southern pied babblers. J
649 Anim Ecol. 81:876-883.
650 Nichols HJ, Cant MA, Hoffman JI, Sanderson JL. 2014. Evidence for frequent incest in a
651 cooperatively breeding mammal. Biol Lett. 10:20140898.
652 Nielsen JF, English S, Goodall-Copestake WP, Wang J, Walling CA, Bateman AW, Flower
653 TP, Sutcliffe RL, Samson J, Thavarajah NK, Kruuk LE, Clutton-Brock TH, Pemberton
654 JM, 2012. Inbreeding and inbreeding depression of early life traits in a cooperative
655 mammal. Mol Ecol. 21:2788–2801.
656 Pakanen V-M, Koivula K, O'Rell M, Rytkönen S, Lahti K. 2016. Sex-specific mortality costs
657 of dispersal during the post-settlement stage promote male philopatry in a resident
658 passerine. Behav Ecol Sociobiol. doi:10.1007/s00265-016-2178-z
659 Peakall R, Smouse PE. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic
660 software for teaching and research - an update. Bioinformatics 28:2537-2539.
661 Perrin N, Goudet J. 2001. Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert
662 J, Danchin E, Dhondt AA, Nichols JD, editors. Oxford: Oxford University Press. p. 123-
663 142.
664 Perrin N, Mazalov V. 2000. Local competition, inbreeding, and the evolution of sex-biased
665 dispersal. Am Nat. 155:116–127.
666 Prugnolle F, De Meeus T. 2002. Inferring sex-biased dispersal from population genetic tools:
667 a review. Heredity. 88:161–165.
668 Pusey AE. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends
669 Ecol Evol. 2:295-299.
670 Pusey A, Wolf M. 1996. Inbreeding avoidance in animals. Trends Ecol Evol. 11:201-206.

671 Queller DC, Goodnight KF. 1989. Estimating relatedness using genetic markers. Evolution.
672 43:258-275.
673 R core-team. 2016. *R: a language and environment for statistical computing*. R foundation for
674 Statistical Computing, Vienna, Austria. http://www.R-project.org.
675 Reed JM, Boulinier T, Danchin E, Oring LW. 1999. Informed dispersal: prospecting by birds for
676 breeding sites. In: Nolan JV, Ketterson ED, Thompson CF, editors. Current ornithology. New
677 York: Kluwer Academic/Plenum Publishers. p. 189-259.
678 Richardson DS, Jury F, Dawson D, Salgueiro P, Komdeur J, Burke T. 2000. Fifty Seychelles
679 warbler (*Acrocephalus sechellensis*) microsatellite loci polymorphic in Sylviidae species
680 and their cross-species amplification in other passerine birds. Mol Ecol. 9:2226–2231.
681 Richardson DS, Jury FL, Blaakmeer K, Komdeur J, Burke T. 2001. Parentage assignment and
682 extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus*
683 *sechellensis*). Mol Ecol. 10:2263–2273.
684 Richardson DS, Burke T, Komdeur J. 2002. Direct benefits explain the evolution of female
685 biased cooperative breeding in the Seychelles warblers. Evolution. 56:2313–2321.
686 Ridley AR. 2012. Invading together: the benefits of coalition dispersal in a cooperative bird.
687 Behav Ecol Sociobiol. 66:77–83.
688 Ridley AR, Raihani NJ, Nelson-Flower MJ. 2008. The cost of being alone: the fate of floaters
689 in a population of cooperatively breeding pied babblers *Turdoides bicolor*. J Avian Biol.
690 39:389-392.
691 Spurgin LG, Wright DJ, Van der Velde M, Collar NJ, Komdeur J, Burke T, Richardson DS.
692 2014. Museum DNA reveals the demographic history of the endangered Seychelles
693 warbler. Ecol Appl. 7:1134-1143.
694 Yaber MC, Rabenold KN. 2002. Effects of sociality on short-distance, female-biased dispersal
695 in tropical wrens. J Anim Ecol. 71:1042-1055.

696 Zack S, Rabenold KN. 1989. Assessment, age and proximity in dispersal contests among
697 cooperative wrens - field experiments. Anim Behav. 38:235–247.

FIGURE LEGENDS

Figure 1. (a) Dispersal distance (minimum number of territories traversed between an individual's natal territory and the territory where they obtained a breeding position) of female (black bars) and male (grey bars) Seychelles warblers, and (b) the mean (±SE) relatedness of the ultimate breeding pairs in relation to the focal individual's dispersal distance. Numbers reflect number of individuals. Females dispersed on average further than males (β = 0.615 ± 0.058, z = 10.67, P < 0.001). However, dispersal distance did not predict relatedness to the obtained partner for both females and males, other than that inheriting individuals (dispersal distance 0) obtained a more related partner than dispersing individuals (see Table 3).

Figure 2. The likelihood that prospecting and floating Seychelles warbler females (black bars) and males (grey bars) died before the subsequent season. Whereas there was no significant difference between prospecting males and females (Fisher exact test: P = 1.00), male floaters were more likely to die than female floaters (Fisher exact test: P = 0.03).

713 **TABLES**

714 **Table 1.** An overview of the concepts of the main hypotheses of sex-biased dispersal in
715 cooperatively breeding birds. A set of predictions was developed to test whether these
716 hypotheses explain female-biased natal dispersal distance in Seychelles warblers. Whether
717 these predictions are met is stated in the final column.

718

Hypothesis	Concept	Prediction in Seychelles warblers (female-biased dispersal)	Prediction met?
Inbreeding avoidance	Dispersal leads to less related partner	Further dispersal leads to a less related partner	No (Fig. 1b)
		Females who disperse to nearby territories have a higher likelihood of engaging in an incestuous relationship (with extra-group father) than females who disperse further	No, locally dispersing females did not obtain a more related partner than far-distance dispersing females (Fig. 1b, Table 3c)
			No, relatedness between short-distance dispersers and their obtained partner was not different between males and females (Fig. 1b, Table 3d)
Resource-holding potential	Territory establishment and defence biased to one sex	Males are more likely to bud off part of their home territory than females	No? Males bud slightly more often than females but not significant ($P = 0.09$), and budding is rare (3.8% of males and 1.3% of females; Table 2)
		Males are larger and heavier than females	Yes, males are 6% larger and 10% heavier
		Females defend less than males	No, females defend equally
Reproductive benefits of philopatry	Sex-biased dispersal driven by sex differences in ability to reproduce as subordinate	Subordinate males reproduce more than subordinate females	No, females reproduce more[1]
	Sex-biased dispersal driven by differences in chance of territory inheritance	Males are more likely to inherit the territory than females	No, equal likelihood (43 vs 41% inherits if a position is available), and only 8.6% of all positions are inherited (Table 2).
		Inheritance improves chance of incest differently between males and females	No, although inheritance improves the chance of incestuous pairing, this was not different between males and females (Table 1b)
		Mothers accept sons as partner more than fathers accept daughters [2]	No, likelihood is equal (35% vs 26%)
		Males expel females after they inherit	No, only 4 of 18 incestuous pairs ended in divorce: in 2 of these the female left, and in 2 cases the male left
Costly dispersal	Costs of dispersal or floating are sex-specific	Sex-bias in reproductive threat of floaters for territory owners	Yes, extra-pair paternity occurs, but no egg-dumping, so that males are more of a threat[1]
		Males are attacked more in foreign territories than females	Maybe: male forayers are attacked twice as much but not significant (limited statistical power)
		Floating males are more likely to die than floating females	Yes, male floaters are 3.5 times as likely to die than female floaters (Fig. 2)

719 [1] 44% of subordinate females lay an egg, but only 1 of 55 young was sired by a subordinate male (Richardson et
720 al. 2001). [2] In species with extra-group mating, the risk of engaging in an incestuous pair after territory inheritance
721 is larger for males than for females, predicting male-biased dispersal. However, since dispersal distance was
722 female-biased in Seychelles warblers, we did not include that hypothesis here.

723

724

725 **Table 2**. The number of subordinate male and female Seychelles warblers (and percentages
726 between brackets) that inherited or budded off part of their natal territory, shifted to a
727 neighboring territory or dispersed further than one territory to their first independent breeding
728 position between 2003 and 2014.

	Inheritance	Budding	Shifting	Dispersal
Males	17 (7.2)	9 (3.8)	75 (31.8)	135 (57.2)
Females	24 (10.0)	3 (1.3)	27 (11.3)	186 (77.5)
Total	41 (8.6)	12 (2.5)	102 (21.4)	321 (67.4)

729

730

731 **Table 3.** The effect of sex and/or dispersal distance on relatedness of Seychelles warbler pairs,
732 when the focal subordinate (a) dispersed, (b) inherited or not, (c) dispersed long vs short
733 distance (females only) and (d) dispersed a short distance.

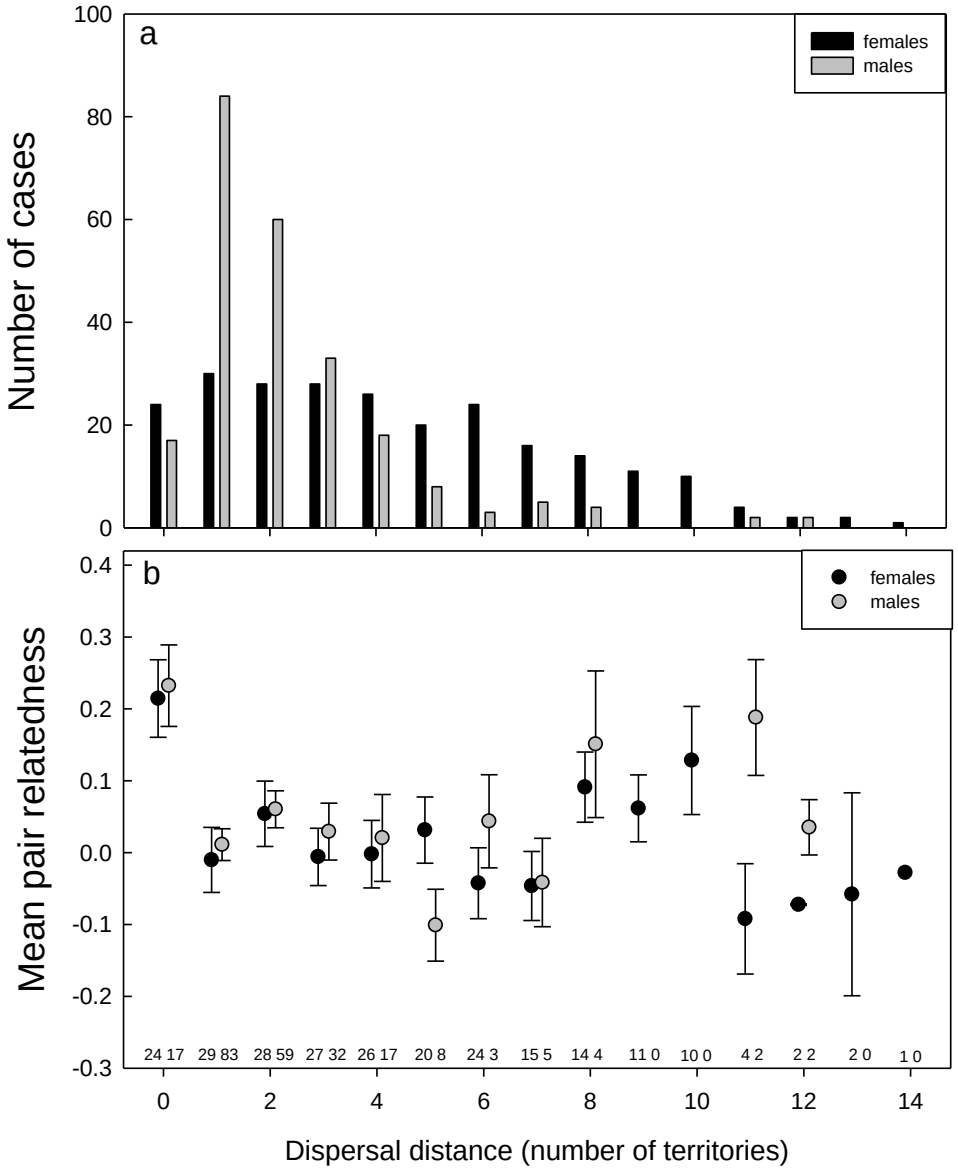
		β	SE	*t*	*P*
a) Relatedness (non-inheriting pairs)	*Intercept*	0.020	0.010		
(428 individuals, 119 territories)	Dispersal distance	0.0005	0.004	0.14	0.89
	Sex	0.016	0.020	0.80	0.42
	Dispersal distance * sex	0.001	0.009	0.12	0.91
b) Relatedness (inheritance vs. dispersal)	*Intercept*	0.020	0.010		
(469 individuals, 121 territories)	Inherited	0.202	0.035	5.75	< **0.001**
	Sex	0.016	0.020	0.81	0.42
	Inherited * sex	-0.002	0.071	-0.03	0.98
c) Relatedness (females only)	*Intercept*	0.011	0.016		
(213 individuals, 90 territories)	Dispersal distance (short vs long)	0.014	0.034	0.41	0.68
d) Relatedness (only short distance)	*Intercept*	0.029	0.015		
(199 individuals, 95 territories)	Sex	0.010	0.033	0.30	0.76

734

735

736 **FIGURES**

737 **Figure 1.**



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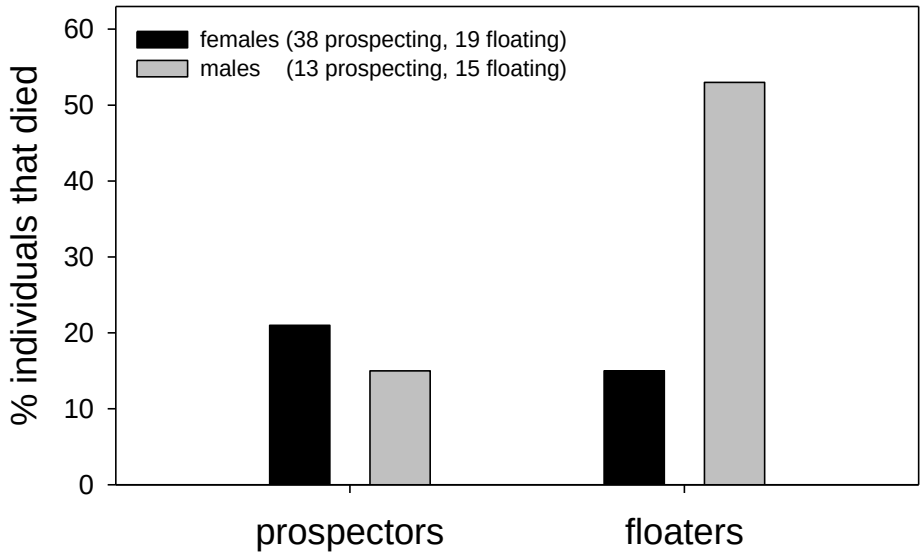
741 **Figure 2.**



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